Demographic vulnerability of an extreme xerophyte in arid Australia

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Callitris glaucophylla is an iconic Australian conifer, but in much of the arid zone there has been little recent regeneration. We found that near Roxby Downs, at the arid extreme of its range, good rain in 2010/11 did not lead to seedling establishment, probably because the wet period was not long enough. Radiocarbon dating showed these trees have a maximum lifespan of about 270 years, which together with instrumental climate records suggests that here, trees of this species have only 2-8 climatic opportunities to reproduce themselves.

Abridged title: Demography of an Australian xerophyte

Abstract

Callitris glaucophylla (syn. *C. columellaris* F. Muell) is an iconic Australian conifer that is suffering a recruitment deficit over much of the arid zone. Here, seedling establishment requires a series of unusually wet years, and protection from high levels of herbivory. The aim of our study was to determine the size class structure of *C. glaucophylla* populations in the most arid part (150 mm mean annual precipitation) of its range, and particularly whether seedlings had established during a wet period in 2010/11. We sampled *C. glaucophylla* populations throughout the region, including inside a 6000 ha feral animal exclosure. We found no seedlings from 2010/11, except on drainage lines adjacent to roads. Of 255 plots centred on mature trees, only 2% contained older seedlings, and 8% contained saplings, with no differences inside or outside exclosure, and 84% of trees were larger than 20 cm basal diameter. Matching dates of known regeneration with long-term rainfall records suggested that successful regeneration of *C. glaucophylla* requires a total of 600-720 mm of rain over a two year period. Our radiocarbon dating showed the age of three large trees ranged from 106 to 268 years, signifying that such trees in this region likely have only 2-8 climatic opportunities to reproduce themselves.

Key words

Arid plant ecology; *Callitris* spp.; conifers; herbivory; population biology; regeneration

Introduction

Callitris glaucophylla (syn. *C. columellaris* F.Muell)(Thompson and Johnson 1986) is an iconic, widespread Australian conifer with a large climatic envelope, including much of arid Australia. Where it occurs in the arid zone, it is often the largest tree and is thus an important structural component of the vegetation. The genus provides valuable habitat for a range of threatened bird species (Maron and Kennedy 2007; Baker-Gabb and Hurley 2011; Garnett *et al*. 2011) and many invertebrates (Major *et al*. 2003), including a restricted, primitive family of moth (Kristensen *et al*. 2015). *Callitris glaucophylla* occupies a range of landscape settings, but in central Australia, it is restricted to topographic fire refugia, reflecting its sensitivity to fire (Prior *et al.* 2010). Although *C. glaucophylla* is one of the most drought-adapted trees on Earth (Brodribb et al. 2010), with highly drought-resistant leaf tissue (Clayton-Greene 1983) and xylem that strongly resists embolism (Larter *et al.* 2017), there are reports of extensive death of mature trees following severe drought (Bean 1910; Sims and Carne 1947), even in the more mesic parts of its range (Harris and Lamb 2004). Historical biogeography suggests this species has expanded and contracted in response to climate change and associated changes in fire regimes (Sakaguchi *et al.* 2013).

Populations of *Callitris glaucophylla* are a useful bio-indicator of environmental change (Prior *et al.* 2011). When conditions are favourable, *C. glaucophylla* can regenerate prolifically, but increased fire frequency or intensity and browsing by introduced herbivores (Cohn *et al.* 2013; Zimmer *et al.* 2017) can cause populations to contract or be eliminated (Prior *et al.* 2011). Arid zone populations appear especially vulnerable to decline (Prior et al. 2011; Cohn et al. 2013). Successful seedling establishment in the arid zone is contingent on a series of unusually wet years (Read 1995), and many arid populations are not regenerating (Prior *et al.* 2011). *C. glaucophylla* seedlings are most vulnerable to drought during their first summer, during which their root system grows quickly, markedly improving their drought tolerance (Zimmer 1944). As well as needing good rainfall during the first year after germination, successful regeneration is also likely to require good antecedent rainfall. Regeneration failure is likely to increase as the climate becomes hotter, evaporation increases and soil moisture availability decreases (IPCC 2014).

C. glaucophylla lacks a long-lived seedbank, and thus its regeneration requires fresh seed being available at the start of a sustained period of high soil moisture. There is marked inter-

annual variation in seed production, even in the wetter parts of its range (Hawkins 1966), and seed viability is highest in heavy seedfall years, amplifying the temporal variation in the amount of fertile seed available (Lacey 1973). The factors contributing to this annual variability are not well understood, but climatic factors undoubtedly play a role, especially in the more arid areas. The total process of seed development, from the first appearance of strobili to release of mature seeds, takes two years (Zimmer 1944), and perhaps up to three years, as has been reported for *C. verrucosa* A.Cunn. ex Endl. (syn *robusta*) (Baird 1953; Lacey 1973; Takaso and Tomlinson 1989). Therefore seedling establishment could be affected by rainfall over a period as long as 4-5 years.

A series of unusually wet years is a necessary but not sufficient condition for *C. glaucophylla* regeneration. Herbivory by both native marsupials and sheep and rabbits is another constraint on the establishment of *C. glaucophylla* seedlings (Zimmer 1944; Johnston 1968; Clayton-Greene and Ashton 1990; Allcock and Hik 2004; Harris and Lamb 2004), especially in arid regions (Prior *et al.* 2011; Cohn *et al.* 2013; Zimmer *et al.* 2017). Arid Recovery Reserve, in arid South Australia, contains an area of 6000 ha from which introduced domestic animals, rabbits, foxes and cats have been removed, and native herbivore species have been reintroduced (Arid Recovery 2017). The recruitment of four woody species has been shown to be greater inside the exclosure from which introduced herbivores had been removed, than in nearby areas where rabbits and cattle were present (Munro *et al.* 2009). We therefore took the opportunity to compare *C. glaucophylla* populations within the exclosure at Arid Recovery Reserve with adjacent populations outside the fence.

Soil condition is also important for seedling establishment. Breaking of the surface crust of soil apparently conserves moisture and provides a suitable medium for germination (Zimmer 1944; Johnston 1968). Early writers have commented on how loose and soft the ground was in drier areas of Australia before sheep were introduced, and how the soil rapidly compacted after their arrival (Bean 1910). Sims (1951) observed that most young *C. glaucophylla* trees were found in hollows where extra water collects. The extensive diggings of small mammals would have produced many such depressions in the landscape, and these would trap seeds, organic litter and water, and thus facilitate establishment of seedlings (Fleming *et al*. 2014). Species of native digging animals such as bilbies, burrowing bettongs, plains mice and stick-nest rats within the feral animal exclosures at the Arid Recovery Reserve could therefore facilitate regeneration of *C. glaucophylla*. However, with few predators, populations of

115 burrowing bettongs (*Bettongia lesueur*) have increased substantially in recent years, to the
116 point where their herbivory could have an adverse effect on vegetation (Arid Recovery 2017).
117
118 Lifespan is another demographic parameter that is critical in predicting the persistence of
119 populations of a long-lived tree that recruits infrequently: the longer the lifespan, the more
120 opportunities a tree has for reproducing and therefore sustaining a population. The lifespan of
121 *C. glaucophylla* is generally regarded as 200 - 250 years (Lacey 1973; Perlinski 1983;
122 Bowman and Harris 1995; Read 1995; Sluiter and Parsons 1995; Cullen *et al.* 2008), but
123 these estimates are based on average growth rates or ring counts that have not been cross-
124 dated. This is problematic because *C. glaucophylla* does not produce annual rings when
125 growing in arid regions (Bowman *et al.* 2011). The best-substantiated estimates of tree age
126 are those by Cullen and Grierson (2009), who developed a tree-ring width chronology and
127 reported ages of up to 397 years for *C. glaucophylla* (syn. *C. columellaris* F. Muell.)
128 growing around salt lakes in arid southern Western Australia (240 mm MAP). However, tree
129 lifespan is likely to be site-specific, so we considered it important to measure tree ages in the
130 Roxby Downs region. We therefore dated three large, well-formed trees from the region,
131 using accelerator mass spectrometry (AMS) ^{14}C dating, following the methods used by
132 Haverkamp *et al.* (2015).
133
134 Our primary aim was to determine whether unusually heavy rain in 2010/11 induced *C.*
135 *glaucophylla* seedling germination, and if so, whether subsequent survival was related to the
136 types of herbivore present. Our secondary aims were to (i) measure the density and sizes of
137 *C. glaucophylla* seedlings and saplings from earlier recruitment events, using information
138 from Read (1995); (ii) relate regional regeneration to rainfall; and (iii) estimate the lifespan of
139 *C. glaucophylla* trees in this region. This study provides the opportunity to reflect on why
140 large tracts of a fire-prone conifer with a regeneration strategy unsuited to extreme aridity can
141 occur in one of Australia's driest landscapes with no obvious topographic fire protection.
142
143 **Methods**
144
145 *Study area*
146
147 The study area is located approximately 550 km north of Adelaide, in the Moondiepitchnie
148 Environmental Association (Read 1995). The area is arid, with 150 to 170 mm mean annual

rainfall, compared with approximately 2800 mm annual pan evaporation (Bureau of Meteorology 2017a). Inter-annual variability in rainfall is high (CV at Arcoona station over 124 years is 47%) (Bureau of Meteorology 2017a). Arcoona Station, in the south of the region, has the longest, most complete rainfall records in the region. Records for Olympic Dam, in the north of the region between Arid Recovery Reserve and the Roxby Downs township, are short and incomplete, but they closely follow patterns at nearby Andamooka township (Appendix 1b). Rainfall patterns are usually consistent across the region (Appendix 1a), but localised thunderstorms occasionally occur, and can be accompanied by heavy rainfall. Such a storm brought rainfall of up to 200 mm to southern parts of the region in January 2007, resulting in the filling of Coorlay Lagoon and Lake Mary (Fig. 1). At Arcoona Station (31.0 °S, 137.0 °E), 190 mm rain fell, while 126 mm fell at Roxby Downs Homestead (30.7 °S, 136.7 °E), compared with only 71 mm at Olympic Dam (30.5 °S, 136.9 °E), about 50 km north (Bureau of Meteorology 2017a). Rainfall was well below average in the north of the region each year from 2005 to 2009 inclusive (the average was 93 mm y^{-1} at Olympic Dam). Following that, a La Niña event in 2010/11 brought above-average rain throughout the region, with Olympic Dam receiving 320 mm in 2010 and 234 mm in 2011.

The *C. glaucophylla* trees in this region grow on low, linear sand dunes, which are generally oriented in an east-west direction (Fig. 1). There is a clay layer within 0.5 to 1.0 m of the top of most dunes in this region, which impedes water infiltration and results in water gravitating along the top of this layer to the dune base (Badman 2002). Soils at the dune base therefore retain a higher moisture content for longer than soils of either dune ridges or swales. This helps to maintain the *C. glaucophylla* that grow on the dunes and send near-surface roots above the clay layer to the dune base, as well as the bands of *Acacia papyrocarpa* that grow along the dune bases. Other tree species on the dunes include *Acacia ramulosa*, *Acacia ligulata* and *Dodoneaea viscosa* ssp. *Angustissima* (Badman 2002). Dune understorey vegetation consists largely of perennial grasses, which are usually sparse in the zone influenced by the trees. Mulga trees (*Acacia aneura*) grow on the dune bases and swales.

Sampling strategy

In May 2015, we sampled areas inside and outside the Arid Recovery Reserve that were known to have large populations of *C. glaucophylla*. The populations we sampled were obvious from roads or minor tracks. Although we tried to remeasure some of the groves

183 measured by Read (1995), we were unsuccessful in finding and identifying any specific
184 groves. Read (1995) did not record locations with a GPS, and there were numerous groves
185 that were very similar to each other in the vicinity of Roxby Homestead. We also thoroughly
186 searched the island in Coorlay Lagoon that was visited by Read, but could not find any live
187 *C. glaucophylla* trees.
188
189 Our demographic study was based on three sampling designs (see below), aimed at recording
190 the general size class structures of *C. glaucophylla* populations in the region, and also
191 characterising regenerating stands of *C. glaucophylla* trees of various sizes. 'Young' trees
192 were considered to be seedlings (<1.5 m high), saplings (≥ 1.5 m high and < 10 cm basal
193 diameter) and erect trees. Saplings develop into small trees with an erect, poplar like form,
194 and only after about 60 years do they become asymmetrical with spreading canopies (Read
195 1995) (Fig. 2).
196
197 There is some subjectivity when measuring density because many trees are multi-stemmed,
198 and it was not always possible to distinguish which stems comprised an individual.
199 Operationally, we considered stems conjoined at ground level to be one individual (although
200 we recognise that some of the stems separated at ground level could also belong to the same
201 individual).
202
203 *Circular plots*
204
205 We established a series of 255 circular plots that spanned the range of the *C. glaucophylla*
206 populations in the study area, in order to measure the size class structure and density of
207 regeneration in mature stands (Fig. 1). To establish the plots, we chose a general direction of
208 travel and walked along the dune, haphazardly selecting a series of mature trees (i.e. with old
209 cones), returning in a similar fashion on the other side of the dune. Care was taken to select a
210 representative sample of tree sizes. Circular plots, 20 m in radius, were then established as
211 described below, with the selected mature trees at their centre. The centre trees were a
212 minimum of 50 m apart to ensure there was no overlap of plots, and at least 100 m distant
213 from major roads and 30 m from any track. Their location was recorded using a GPS.
214
215 Within each plot we measured the height and basal diameter of the centre tree, and whether
216 developing cones were present. Basal diameter (BD), rather than diameter at breast height,

was measured because most trees in the region are multi-stemmed. There are good relationships between BD and diameter at breast height for single-stemmed trees and between BD and tree height in this region (Appendix 2). The height of the centre tree was measured using a hypsometer (Vertex IV with T3 transponder; Haglöf, Långsele, Sweden). We then counted the number of trees in each plot in the following five size classes: seedlings (< 1.5 m high); saplings (≥ 1.5 m high and < 10 cm BD); 10 – 20 BD; 20 – 40 cm BD and ≥ 40 cm BD. Basal diameter was measured with a diameter tape, and distance from the centre tree was measured using ultrasound (DME 201 Cruiser; Haglöf, Långsele, Sweden). The soil surface was predominantly bare at most sites, which facilitated the search for seedlings and saplings. We paid particular attention to fallen branches or shrubs that could potentially shelter regeneration. For all seedlings and saplings, the position, height, diameter class, distance to the nearest mature tree and presence of cones (old or developing) were recorded.

Field traverses

We also measured 'young' trees (seedlings, saplings and erect trees) encountered while traversing the dunes between the circular plots, to determine where regeneration occurred in relation to mature trees (young trees > 20 m distant from mature trees would not be captured by the circular plots). This also boosted the number of 'young' trees in our analyses of presence of cones in relation to tree size. On most dunes, 'young' trees were sparse, and we measured all we saw within ~50 m of our traverse, but in the few instances where there were very large patches of regeneration, we measured a representative sample of ~10 trees.

Regeneration transects

There were extensive populations of older regeneration, predominantly in the south of our study region, which were documented by Read (1995) as establishing in 1946, 1949 and 1974. Size class structures of four of these populations were measured using transects that were 10 m wide and 35 - 50 m long. Similarly, many large seedlings and saplings were observed growing on drainage lines at the edge of the sealed highway, and to measure these, another four regeneration transects 10 m wide, and 25 – 50 m long, were placed at the edge of the highway. The height, diameter class, presence of cones and, for the roadside transects, distance from the road were recorded for all trees within these transects.

Tree ages and growth rates

Two wood cores with 5 mm diameter were sampled from stems of 45 well-formed, single-stemmed trees across the region in 2009 (Prior *et al.* 2012). We selected three of the longest, most intact cores for growth ring analysis and AMS ^{14}C dating. Radiocarbon dating of single samples cannot be used to precisely date trees that established between 1650 and 1950 AD (Hua 2009). In addition, the rings of these trees are too narrow to supply enough material for the validation of their individual tree-ring ages using the bomb-pulse radiocarbon method, as has been used in some other *Callitris* trees (Bowman *et al.* 2011; Pearson *et al.* 2011). Instead, we used multiple samples to derive a series of dates along the growth axis of each tree to reduce uncertainties associated with each ^{14}C calibrated age, and thereby improve the precision of calibrated ^{14}C dates, as was recently done for *Callitris sulcata* trees, which also have very narrow rings (Haverkamp *et al.* 2015). Five samples of wood collected along the growth axis of each tree were pre-treated to extract alpha-cellulose using the methods described in Hua *et al.* (2004). Alpha-cellulose was then combusted to CO_2 and reduced to graphite (Hua *et al.* 2001) for ^{14}C analyses using the STAR AMS facility at the Australian Nuclear Science and Technology Organisation (ANSTO; Fink *et al.* 2004). Age calibration was performed using OxCal 4.2 (Bronk Ramsey 2009) with bomb radiocarbon data for the Southern Hemisphere Zone 1-2 (Hua *et al.* 2013) extended back in time using the SHCal13 data (Hogg *et al.* 2013). We employed the "Simple Sequence" deposition model of the OxCal calibration programme (Bronk Ramsey 2008) for chronological reconstruction using the chronological ordering constraint (outer samples are younger than inner samples). The same calibration data were used for both unmodelled and modelled calendar ages.

Average growth rates of the three trees at sample height (41 to 84 cm) were calculated from the distance to bark from the innermost sample and the corresponding AMS ^{14}C dates. The time taken to grow to sample height was estimated from height growth data for *C. glaucophylla* seedlings in semi-arid Victoria (10 cm year^{-1}; Zimmer 1944), and added to the ^{14}C dates to give total tree age. Average BD increment was calculated from this and BD. Similarly, average increment in diameter at breast height was calculated assuming the tree took 13 years to attain 1.3 m height.

Statistical analyses

We used generalised linear models (glm) and model selection based on Akaike's information criterion (AIC) to test statistical support (Burnham and Anderson 2002). We considered a model was statistically supported if it received an Akaike weight > 0.73 (Murphy et al. 2010). The software package R was used for all analyses (R Core Team 2016). For seedling and sapling presence in the circular plots, we compared binomial models containing the term 'location' (inside vs outside the Arid Recovery Reserve) with the null (intercept only) model to test the effect of non-native animal exclusion. For sapling density we used a zero-inflated Poisson model of sapling counts in each plot using the package 'pscl' (Jackman 2015), and compared the 'location' model with the null model. There were too few plots with seedlings to analyse seedling densities. To derive the relationship between presence of cones and height of 'young' trees, we used a binomial glm.

Results

Tree density and regeneration

Average *C. glaucophylla* density in the circular plots was 39.8 ± 2.3 (se) trees per ha (Table 1). This is an over-estimate of overall density on the dunes because many areas of dune have no *C. glaucophylla* trees, and our plots were always centred on a tree. There was a strong predominance of large trees in the circular plots (Fig. 3). Of these trees, 45% were > 40 cm basal diameter, and a further 39% were 20 to 40 cm basal diameter. Only 2% of the circular plots contained seedlings, and 8% contained saplings. There were no differences in the presence or density of seedlings and saplings on either side of the feral animal exclosure (Table 1).

The size class distributions in the regeneration transects were consistent with these stands having regenerated in a single event (Fig. 4), as shown by the marked peak at a particular size. The Roxby HS transects A and B had a very similar size class structure, with most trees in the 10 to 20 cm BD class. In the Roxby HS transect C, most trees were in the 20 to 40 cm BD class, suggesting an earlier regeneration event, while at Lake Mary, most individuals were in the seedling and sapling size classes, and had presumably established more recently. The roadside transects, where we targeted stands of small individuals, also consisted mostly of seedlings and saplings (Fig. 4).

Overall, 85% of 'young' trees encountered in our field traverses of the dunes were between 15 and 35 m from the nearest mature tree (Fig. 5). Only 7% of 'young' trees were within 10 m of mature trees, and only 4% were >40 m distant.

A few very short trees (< 1 m high) had cones present, but it was not until trees attained a height of 3 m did half of them have cones (Fig. 6). Although old, open cones without seed were present on all centre trees, new developing cones were detected on only 16.5% of these trees. The presence of new cones on the centre trees was not related to either tree height or basal diameter.

^{14}C dating, growth rates and tree ages

The ^{14}C dating indicated that the innermost wood samples from the three large trees were 260, 155 and 102 years old (with associated 1σ uncertainties being 40, 63 and 67 years) when the cores were taken in 2009 (Table 2; Appendix 3). Using the value of 10 cm year^{-1} for juvenile height growth, we estimated these trees were 268, 162 and 106 years old. Basal diameter growth rates calculated from these ages were 2.1, 3.1 and 4.7 mm year^{-1} respectively (average 3.3 mm year^{-1}; Table 2), and thus showed large inter-tree variability.

Assuming juvenile height growth of 10 cm y^{-1} means our 'seedlings' are < 15 years old, and thus established after the year 2000. Using the average basal diameter growth of 3.3 mm y^{-1} (Table 2), we estimated the establishment dates corresponding to our basal diameter class thresholds as 1985 (10 cm BD), 1954 (20 cm BD) and 1894 (40 cm BD). Of the 1019 trees (including juveniles) that we measured in the 255 plots across the region, we therefore calculate that nearly half of individuals germinated before ~1894. More than 80% of the trees had a basal diameter > 20 cm, corresponding to an establishment year before 1954 (Fig. 3). Only 5% of individuals established after 1985.

Discussion

Callitris glaucophylla populations in the Roxby Downs region are growing at the arid extreme of their climatic envelope (Prior *et al.* 2011). The density of trees found in the current study was within the sparsest part of the range reported for *C. glaucophylla* trees growing in other areas of arid Australia (Prior et al. 2011). Our age estimates of three large

353 trees were all < 270 years, which is considerably younger than the 397 years for the oldest
354 tree at Lake Tay, in southern Western Australia (Cullen and Grierson 2009). Our *C.*
355 *glaucophylla* trees were also far younger than some of the rare New Caledonian species,
356 *Callitris sulcata*, which has a lifespan of 560 years or more (Haverkamp *et al.* 2015). We
357 estimated average BD growth rates of *C. glaucophylla* in the Roxby Downs region at 0.21 to
358 0.47 cm year^{-1}, which was faster than we expected, given the very arid climate. Reasonably
359 fertile and deep soils and a lack of competition presumably contribute to fast growth
360 following good rain events. By comparison, *C. sulcata* grew at only 0.09 to 0.15 cm year^{-1}
361 (Haverkamp *et al.* 2015), despite growing in a much milder, wetter climate, probably because
362 it has to contend with shallow ultramafic soils.
363
364 Although grazing can reduce or eliminate establishment of *C. glaucophylla* seedlings,
365 especially in arid environments (Cohn *et al.* 2013; Zimmer *et al.* 2017), we found no
366 differences in recent recruitment inside and outside of the exclosure. This suggests herbivory
367 by introduced animals was not the primary cause of the lack of recruitment during the 2011
368 wet period. Other studies of tree regeneration in arid Australia have also shown mixed results
369 following herbivore exclusion (Zimmer 1944; Zimmer *et al.* 2017). It is also possible that the
370 high numbers of herbivorous native marsupials constrained regeneration inside the exclosure
371 after this wet period (Arid Recovery 2017). Within the fenced reintroduction areas, both
372 greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*) consume and
373 redistribute seeds, as well as consuming plant material (Newell 2009).
374
375 Seedling establishment is the tree demographic process most likely to be limited by climate
376 because seedlings are small and have access to very few resources (Eriksson and Ehrlén
377 2008). Zimmer (1944) observed that *C. glaucophylla* seedlings are most vulnerable to
378 drought during the first year after germination, but invest heavily in root growth, which
379 confers strong drought resistance in older seedlings. The only seedlings we observed from the
380 recent high rainfall La Niña period in 2011 (when the 24-month running average peaked at
381 23.9 mm) were growing at the side of the road, where they receive extra run-off. We also
382 observed some older seedlings in the south of the region, apparently as a result of a localised
383 thunderstorm in January 2007, which dumped up to 200 mm rain. In the centre of the region,
384 there are numerous regenerating stands dating from unusually wet periods in the 1940s and
385 the 1970s, but in the north (in and adjacent to the Arid Recovery Reserve), there were few
386 trees smaller than 20 cm, corresponding to establishment since 1954. The scarcity of

developing cones on mature trees, combined with the lack of a persistent soil or canopy seedbank (Lacey 1973), suggests that seed availability could be an important constraint on regeneration in this region.

We found that 85% of regeneration occurred between 15 and 35 m of the nearest mature tree, consistent with Read's (1995) observation that seedlings usually do not establish within 12 m of an existing tree. This means that opportunities for seedlings to establish on dunes with existing *C. glaucophylla* populations are limited, and that potential for the densest regeneration is on areas with sparse mature trees. Indeed, the prolific stands of older regeneration near Roxby Homestead appeared predominantly single-aged, with few trees > 20 cm basal diameter, as Read (1995) also observed. It could be common in this region for whole stands to originate during unusually favourable conditions, and eventually succumb to drought or old age without producing replacement trees. Thus stands could flicker in and out of existence throughout the landscape, rather than persisting for generations in the one location. This would depend on the survival of some mature trees as a seed source until at least the next exceptionally wet period, perhaps in the parts of the dune system that receive unusually large amounts of seepage or run-on. Movement of populations between dunes also requires seed dispersal beyond the usual close proximity to the parent tree, possibly by means of convectional whirlwinds (Lacey 1973). This dependence on unusual weather events would result in a regional *C. glaucophylla* distribution that is very sensitive to climate change, and vulnerable to local extinction.

The absence of a long-lived seedbank, and requirement for several successive 'wet' years for seed production and establishment, renders this species vulnerable as climate condition become more arid. *C. glaucophylla* populations in the Roxby Downs region are dominated by old trees, with 45% > 40 cm basal diameter, a size that takes an average of 150 years to attain. Our results show that the maximum lifespan of *C. glaucophylla* in this region is about 270 years, which is broadly consistent with Perlinski's (1983) value of 250 years. Therefore most of these large, old trees are likely to die within the next ~120 years, even without major disturbance such as severe drought or fire. Widespread recruitment across the region will be needed to replace these trees. There appeared to be only about three climatic opportunities for widespread seedling recruitment during the 20th century. These limited opportunities could be further reduced by decreasing water availability as a result of climate change. Indeed, this region has experienced recent trends of decreasing rainfall (approximately 10 mm/decade

between 1970 and 2016), combined with increases in evaporation (Bureau of Meteorology 2017b), and winter rainfall is projected to decrease in the future (Australian Government 2017).

Matching dates of known regeneration (Read 1995) with long-term rainfall data suggests that successful regeneration of *C. glaucophylla* can only occur if 24-month running average rainfall exceeds 20 mm, and probably requires 25-30 mm (*i.e.* a total of 600 – 720 mm rain needs to fall in a 2-year period for successful establishment to occur). There were three such periods between 1890 and 2016 in the Roxby Downs region (Fig. 7). Assuming our three sampled trees capture the range of longevity for this species, and that long-term rainfall patterns are similar to those of the historical period, individual trees would have only between two and eight opportunities during their lifetimes to reproduce and replace themselves. The extreme marginality of the Roxby Downs region for *C. glaucophylla* regeneration is evident when it is compared to other arid regions where the species is found (Fig. 8). During the period 1900-2010, the three occasions in the Roxby Downs region when the 24-mo moving average rainfall exceeded 25-30 mm compares with more than 10 occasions in all of the Kalgoorlie (southern Western Australia), Wentworth (south-western New South Wales), and Alice Springs (central Australia) regions. Moreover, these occasions were sustained for much longer in other regions, especially around Alice Springs (Fig. 8).

It is likely that in central Australia, fire is a much more important constraint on *C. glaucophylla* populations than it is in the Roxby Downs region (Bowman and Latz 1993; Prior *et al.* 2010). The central Australian arid region receives occasional heavy monsoonal rain, and has considerably more fire activity than the southern arid region (Russell-Smith *et al.* 2007). In central Australia, periods with unusually heavy rainfall are often followed by extensive, severe fires as grassy fuels produced in the wet period cure and become highly flammable (Murphy *et al.* 2013). Thus fires burn at the very time when the very fire-sensitive *C. glaucophylla* seedlings need to establish. Indeed, in central Australia, *C. glaucophylla* is largely confined to fire-protected refugia, whereas in southern arid areas, it is frequently found on extensive sand dunes and sand sheets (Prior *et al.* 2011). Thus the extensive tracts of *C. glaucophylla* in landscapes with no topographic fire protection near Roxby Downs can be understood as effectively occupying fire refugia in the form of areas with low loads of usually discontinuous fuels associated with chronic, severe drought. Our argument

concerning a climatic fire refugium explains the paradox of why a species can occur in the driest region of Australia despite a regeneration strategy that is unsuited to extreme aridity.

At a palaeoecological time scale, *C. glaucophylla* populations in inland Australia have fluctuated in response to climate, fire regimes and, more recently, changes in human populations (Luly 1993, 2001; Cupper *et al.* 2000; Thomas *et al.* 2001; Sakaguchi *et al.* 2013). Palynological studies show that *C. glaucophylla* woodlands were widespread in the region around Lake Eyre and Lake Frome, in arid South Australia (approximately 50-100 km from our study region), between 30,000 and 50,000 years ago (Luly 2001). However, a drying and cooling climate in the lead up to the Last Glacial maximum apparently destroyed the tree vegetation in the region, and *C. glaucophylla* retreated to wetter, topographically protected refugia in the nearby Flinders Ranges. Subsequent expansion was rapid during post-glacial climatic amelioration, but then a second decline occurred, coincident with an increase in both charcoal particles and human populations (Luly 2001). Range contractions during the Last Glacial Maximum (*ca* 20,000 years ago) were also supported by species distribution modelling and genetic demographic analyses, which showed that arid *C. glaucophylla* populations experienced strong bottlenecks around this time (Sakaguchi *et al.* 2013). Such dynamics support the idea that *C. glaucophylla* can persist in extremely arid areas without topographic fire protection because of the low occurrence of fire, but in areas where the climate is less harsh, the species is restricted to areas that physically exclude fire (Prior et al. 2011). Thus *C. glaucophylla* is vulnerable to both increased water availability increasing fuel loads and the probability of fire, and to decreased water availability reducing the opportunities for recruitment. It appears to occupy a small niche with specific requirements regarding topography (in moderately arid areas) and the amount and timing of rainfall (in the most arid areas). Within the next few centuries, *C. glaucophylla* populations could once again disappear from the Roxby Downs region, while those in the Flinders Ranges region, which is wetter and also contains fire refugia, are more likely to persist.

Acknowledgements

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Conflict of interest

The authors declare no conflicts of interest.

Supplementary material

Figures and table showing 24 month moving average rainfall for various stations in the Roxby Downs region; relationships between basal diameter, diameter at breast height and tree height; and radiocarbon results.

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731

Table 1. The percentage of the 255 circular plots with seedlings (< 1.5 m tall), saplings (< 10 cm basal diameter), and trees in the 10 to 20 cm, 20 to 40 cm and > 40 cm basal diameter classes, and the density of trees in each class (includes centre trees).

The data for seedlings and saplings inside the feral animal exclosure at Arid Recovery Reserve (66 plots), and adjacent dunes outside the exclosure (31 plots), is also shown. We considered there was statistical support for differences between inside and outside the exclosure if w_i exceeded 0.73 (Murphy et al. 2010). There were insufficient seedlings to analyse differences in density. We did not test for differences in trees > 10 cm BD because they would have established prior to the erection of the exclosure.

	seedlings	saplings	10-20 cm BD	20-40 cm BD	>40 cm BD
		Presence (% plots)			
All circular plots	2	8	17	53	91
Arid Recovery Reserve – inside exclosure	0	11			
Arid Recovery Reserve – outside exclosure	3	6			
w_i –inside vs outside	0.53	0.31			
		Density (ha^{-1})			
All circular plots	0.5	1.4	3.6	14.2	20.1
Arid Recovery Reserve – inside exclosure	0	0.8			
Arid Recovery Reserve – outside exclosure	0.3	0.5			
w_i –inside vs outside	n.a.	0.31			

744 **Table 2. Summary of age and growth rate calculations for the three large, well-formed**
745 ***C. glaucophylla* trees sampled for AMS ^{14}C dating.**
746 The full results of the AMS ^{14}C dating are presented in Appendix 3.
747

Core	Basal diameter	Hole height	Diameter at hole height	Year - Calibrated	Age in 2009	1σ	Time to hole ht	Total age	Diameter increment at		
									Base	Hole height	Breast height
	cm	cm	cm	AD	y		y	y	cm y^{-1}	cm y^{-1}	cm y^{-1}
RD1_3B	56.5	84	50.0	1749	260	40	8	268	0.21	0.19	0.19
RD2_9B	50.5	68	46.5	1854	155	63	7	162	0.31	0.30	0.29
RD3_2A	50.0	41	41.5	1907	102	67	4	106	0.47	0.41	0.41
Average	52.3				172		6	179	0.33		0.30

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749

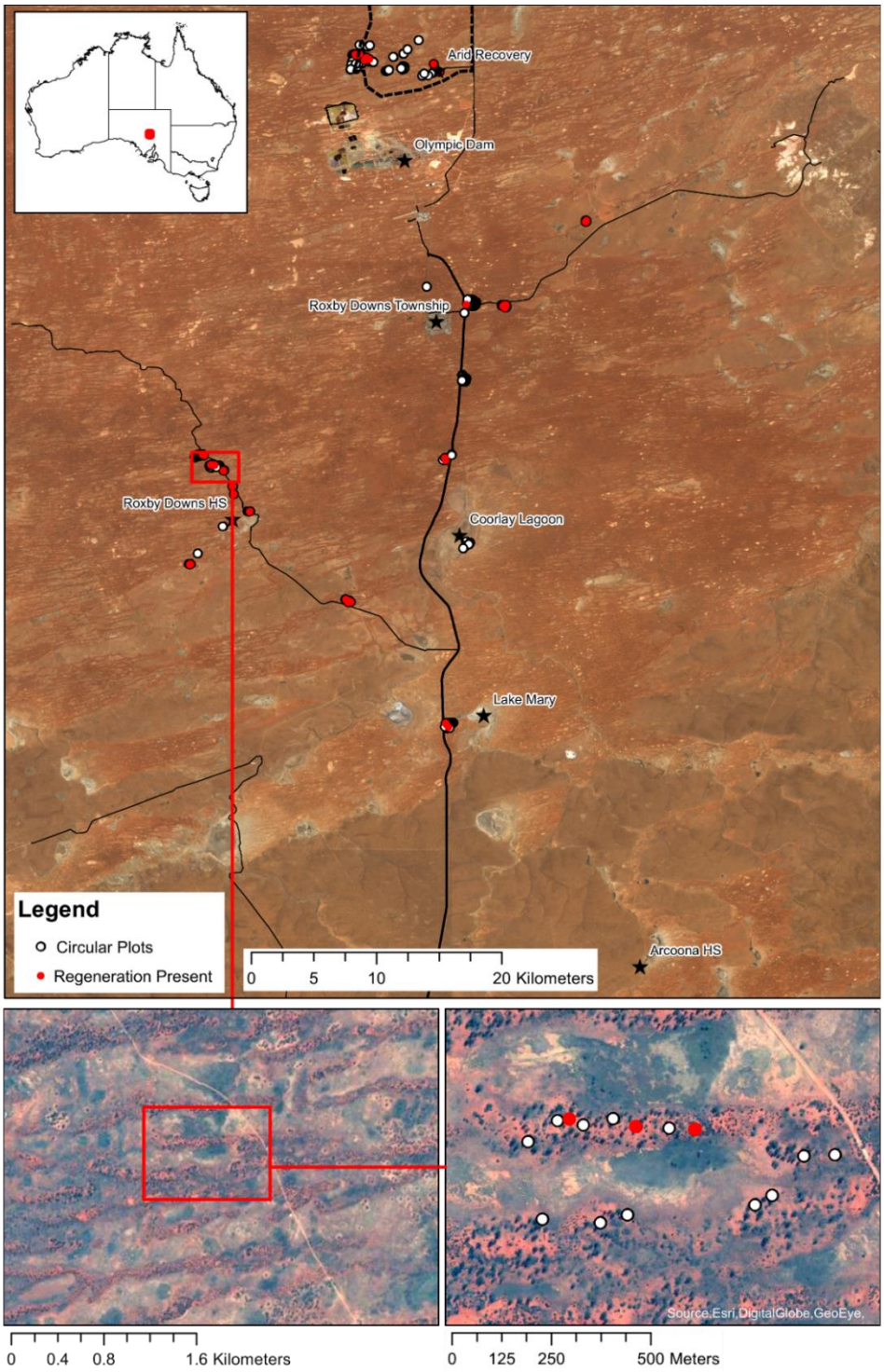


Fig. 1. Locations of plots (open circles), and where young trees were recorded (solid red circles). Many symbols have been super-imposed where transects were close together. 'Young' trees were considered to be seedlings, saplings and 'erect' trees with a poplar-like form. Stars indicate localities, and "HS' indicates homestead. Lower panels show the tree cover on the longitudinal dunes in the region. Most of the individual trees discernible in the lower right panel are *C. glaucophylla*.

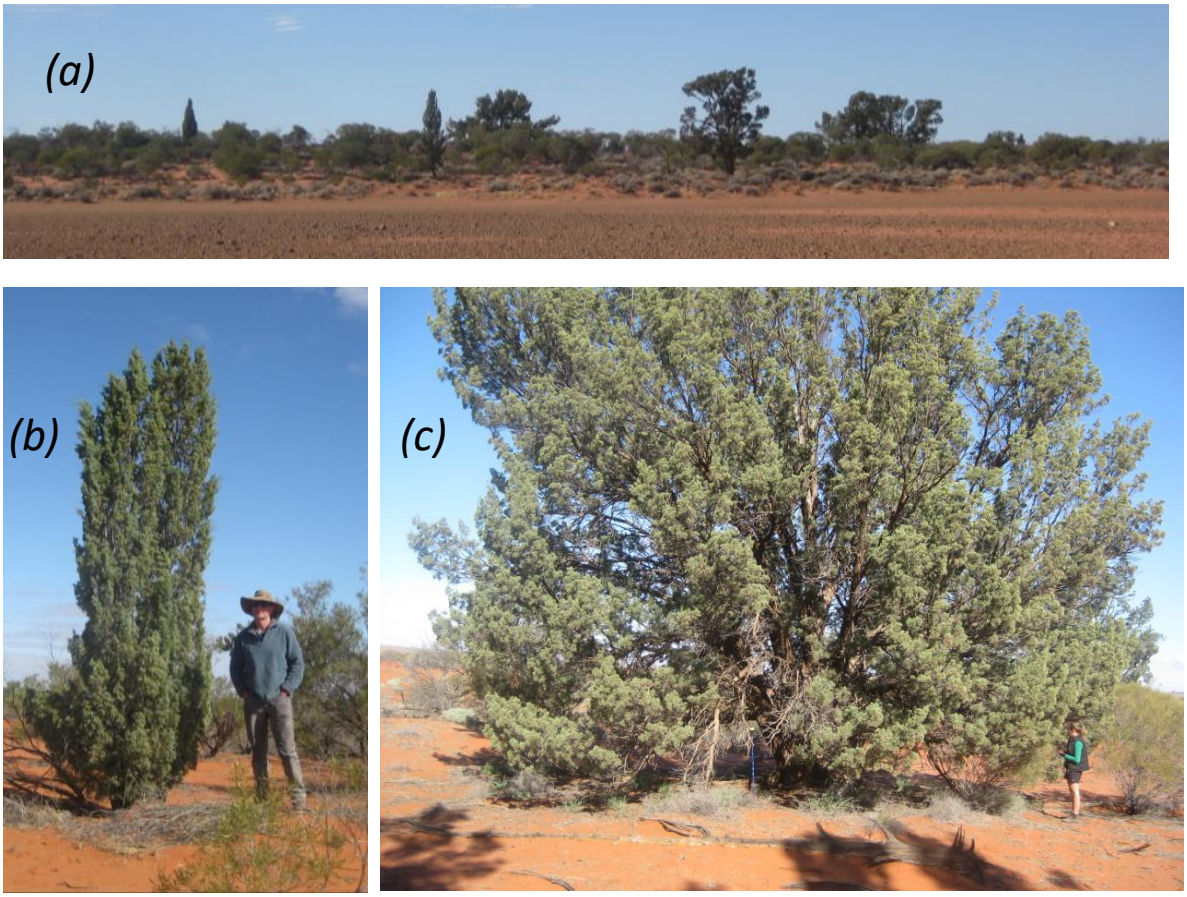
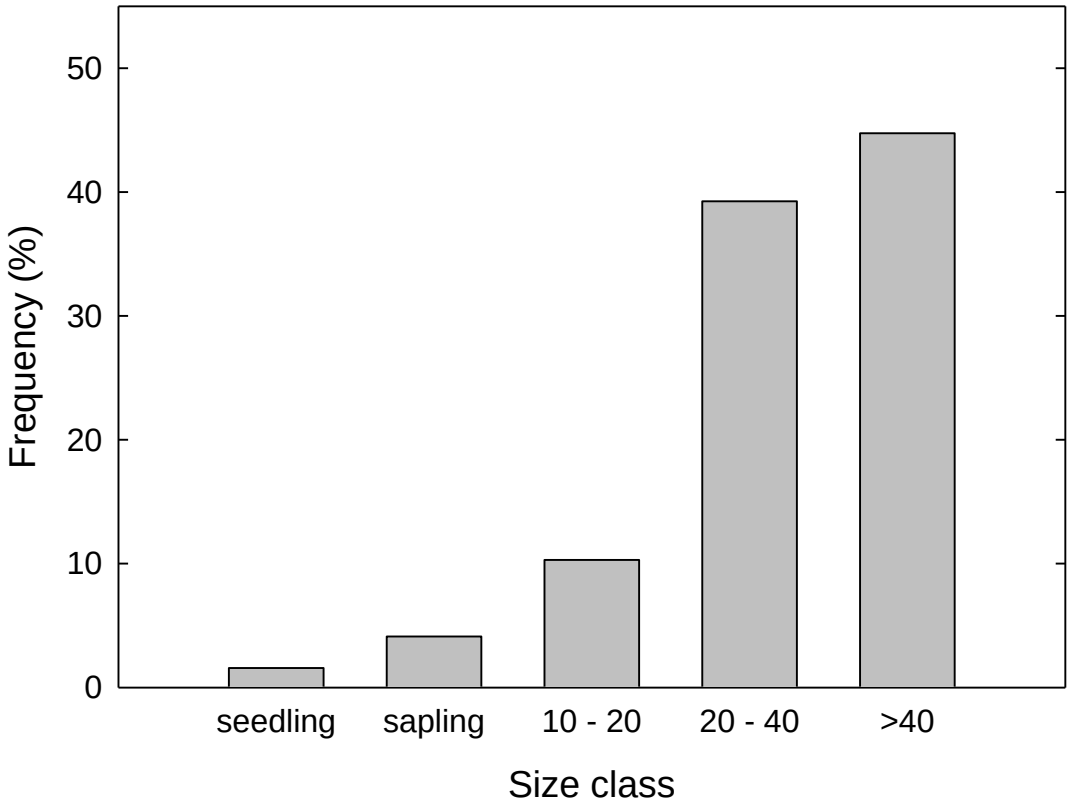


Fig. 2. *(a)* Comparison of the erect, poplar-like form of the two 'young' trees (less than about 60 years old; Read 1995) on the dunes in the left of the photo, with the spreading form of the three mature trees on the right, *(b)* a young, erect tree, and *(c)* a very large, healthy mature tree. Photographs by L. Prior.

765



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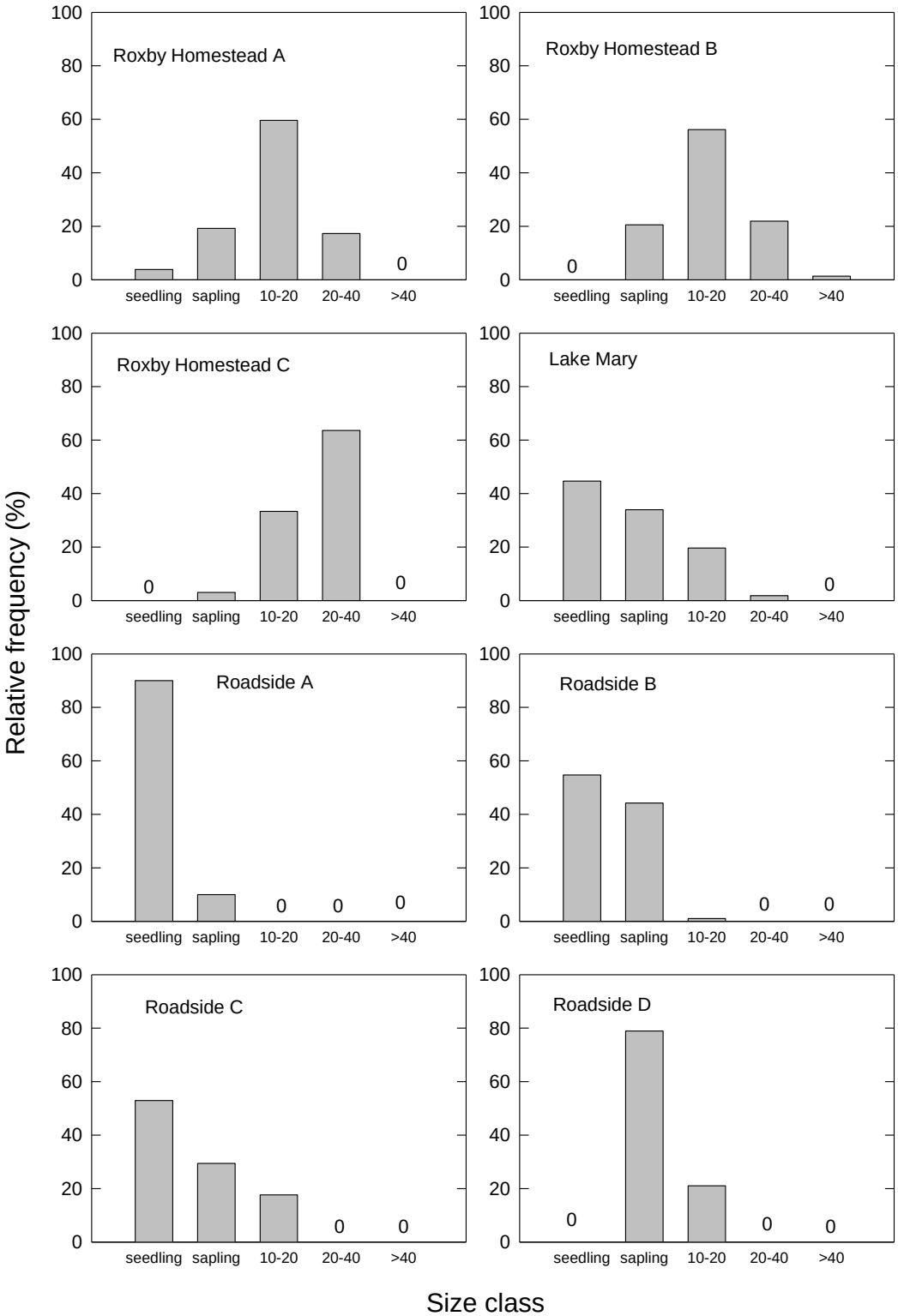
767

768 **Fig. 3.** Relative frequency distribution of size classes of trees in all the circular plots
769 combined (excluding the central trees, which were over-represented by large sizes). Size class
770 refers to seedlings (<1.5 m high), saplings (>1.5 m high and < 10 cm BD) or basal diameter
771 range (in cm).

772



773

774 **Fig. 4.** Relative frequency distribution of size classes of trees in the regeneration and the
775 roadside transects. Size class refers to seedlings, saplings or basal diameter range (in cm).
776 Most trees in the Roxby Homestead C transect were transitioning from young, erect
777 symmetrical trees to more spreading adult trees.

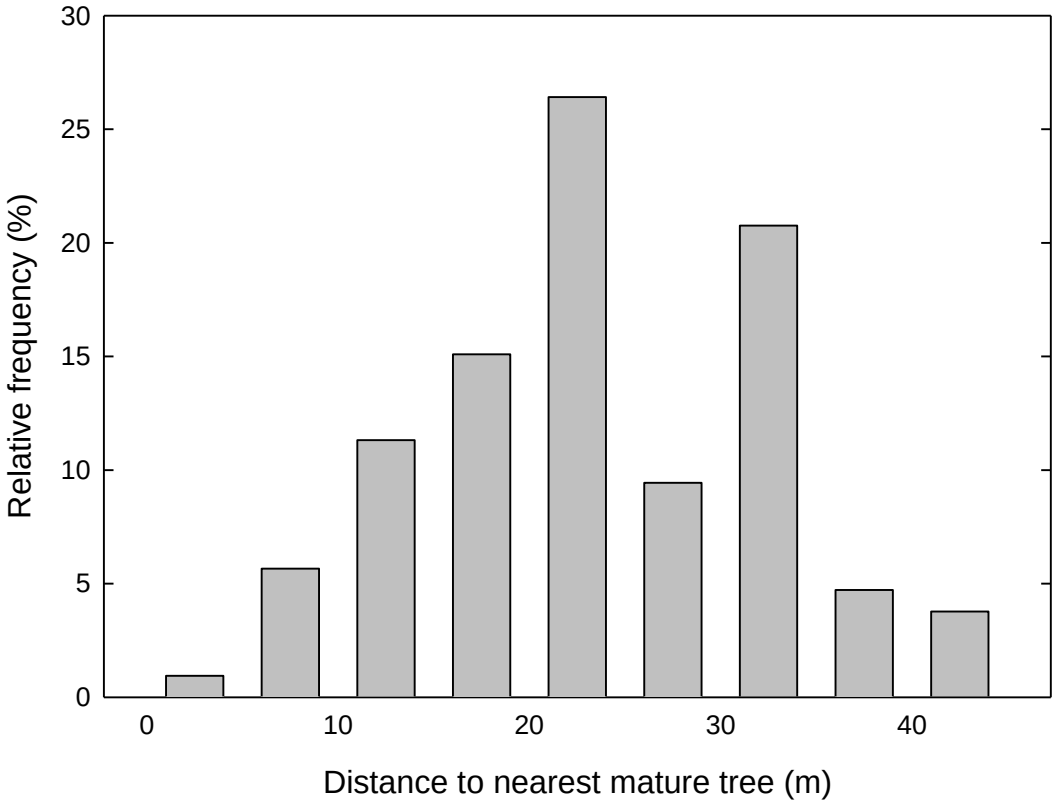
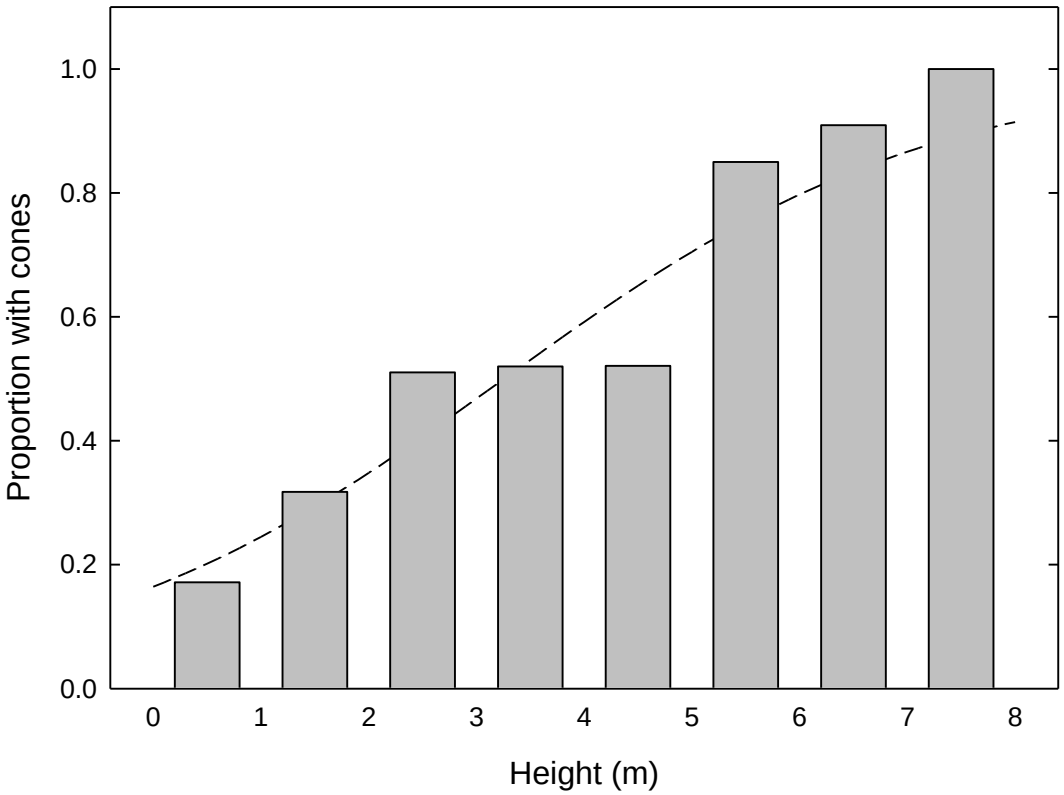


Fig. 5. The relative frequency of distance from mature trees (with cones and the 'mature' form) for 'young' trees (seedlings, saplings and small trees with an 'erect' form). These are results of our field traverses, where we used consistent effort to detect and record 'young' trees. (We did not use trees inside the circular plots, to avoid inflating the results with trees < 20 m distant from a mature tree, where our search effort was much more intensive.)



790

791 **Fig. 6.** The proportion of 'young' trees with cones (old or developing) as a function of height.
792 The dotted line indicates the fit of the binomial generalised linear model (glm). Trees are
793 binned into 1-m height class for presentation, but continuous data were used in the modelling.
794 'Young' trees were considered to be seedlings, saplings and 'erect' trees with a poplar-like
795 form.

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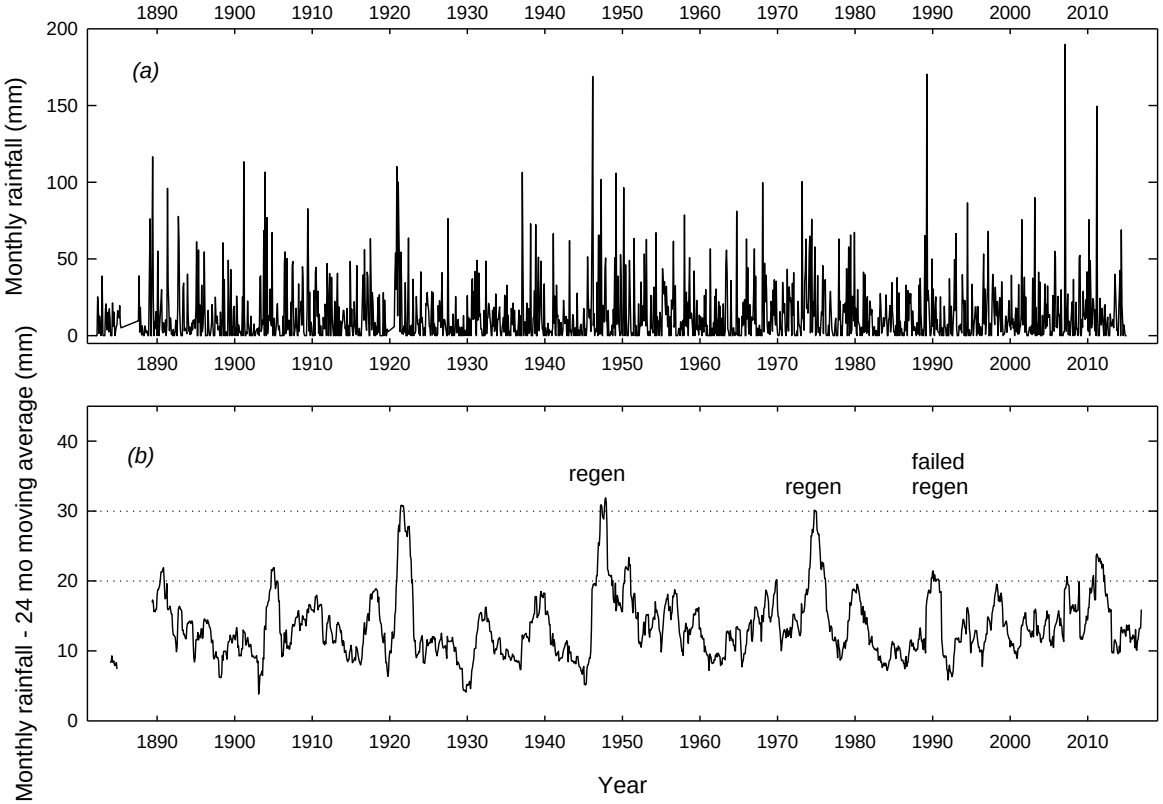


Fig. 7. *(a)* Monthly rainfall at Arcoona, the station in our study region with the longest and most complete rainfall record. When Arcoona data were missing, data from Roxby Downs Homestead (or if that not available, Parakylia Station), were used. *(b)* 24-month moving average rainfall at Arcoona; values of 20 and 30 mm rain per month are shown by the dotted lines. Periods of *C. glaucophylla* regeneration (i.e. late 1940s and 1974; Read 1995) are shown. Read (1995) also documented regeneration soon after good rain in March 1989, but germinants did not survive the following dry period and were all dead by October 1990. We infer from this that an average of 25-30 mm rain per month over 24 months is needed for *C. glaucophylla* to successfully establish. This figure shows there were three such periods between 1890 and 2016 in the Roxby Downs region, in the early 1920s, the late 1940s and the mid 1970s. It is unknown whether regeneration occurred in the 1920s.

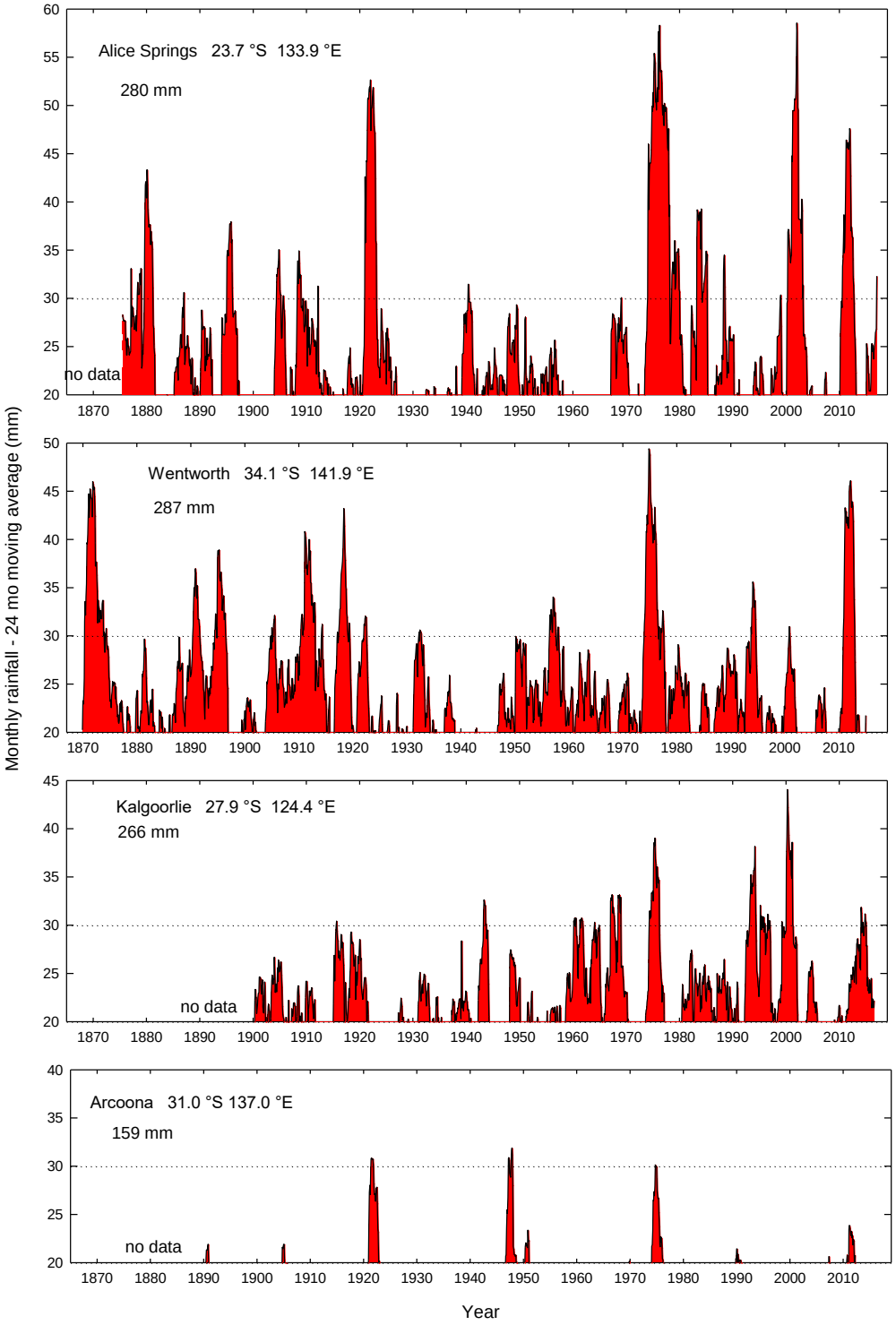
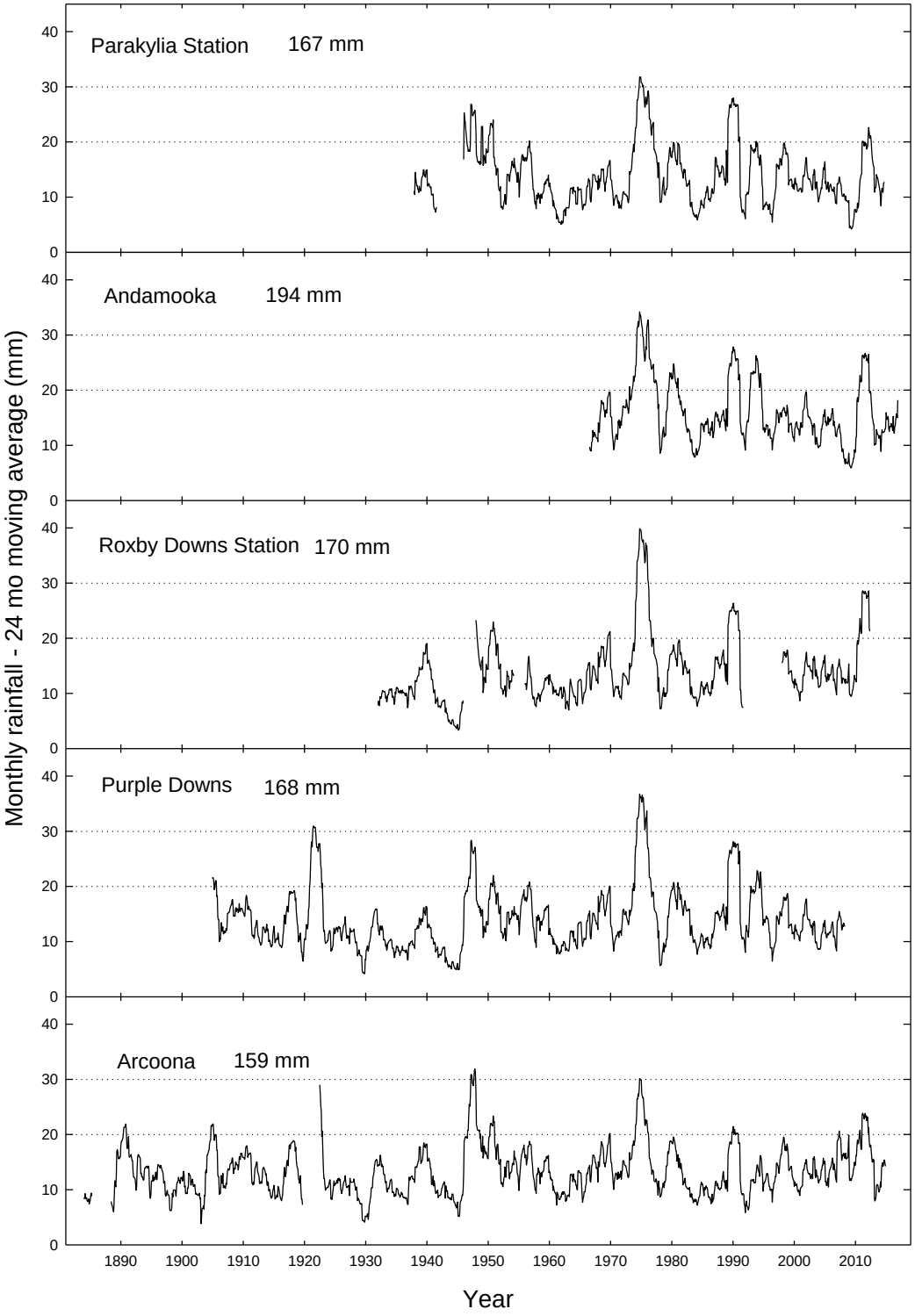
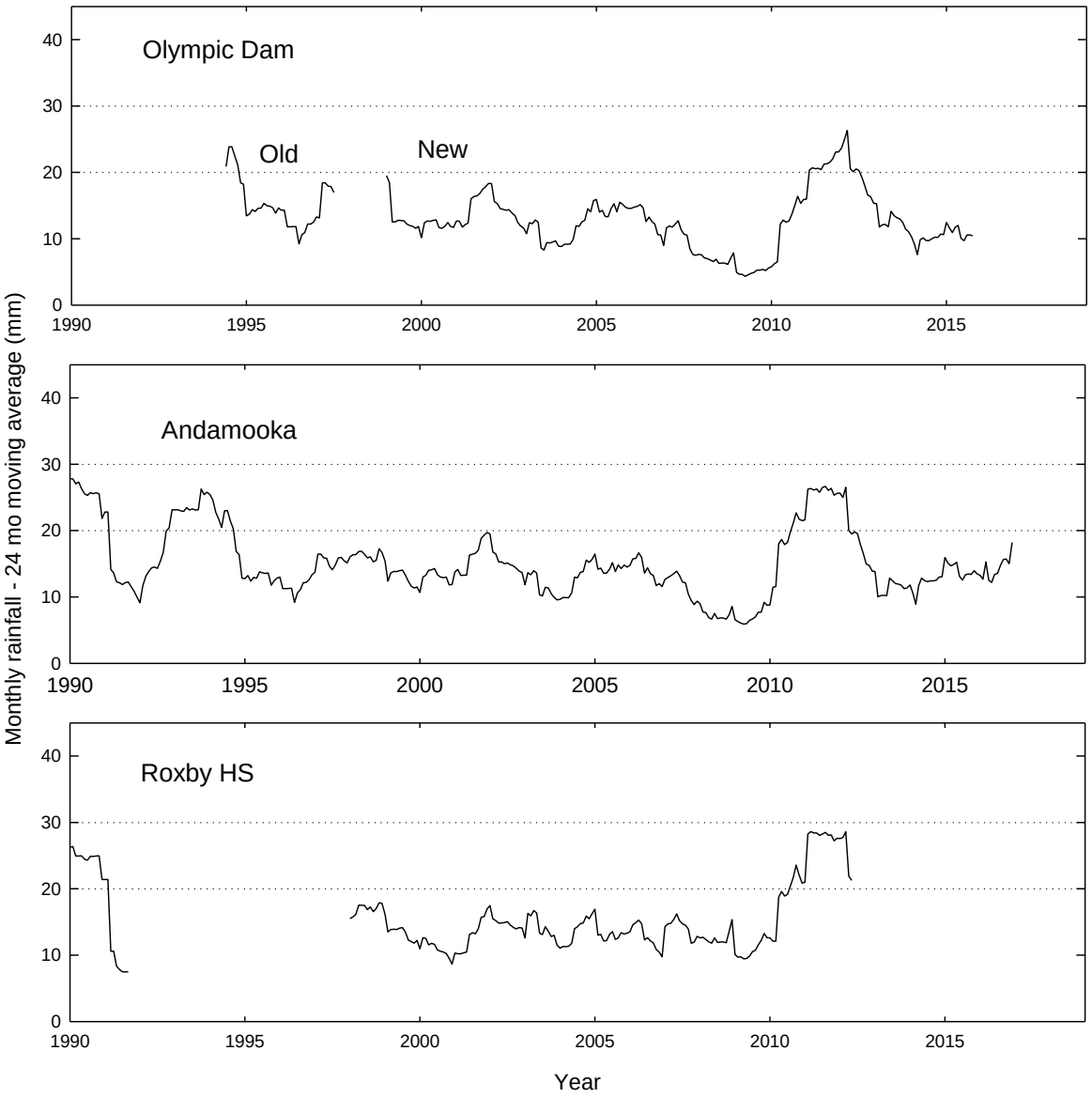


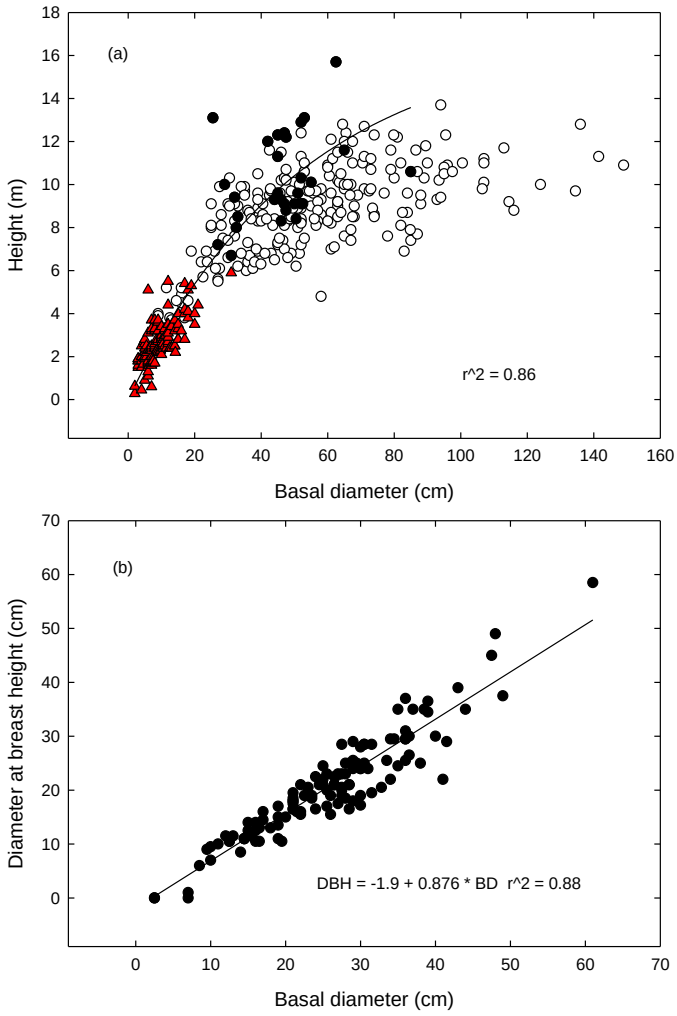
Fig. 8. 24-mo moving average rainfall at Arcoona (Roxby Downs region) compared with four towns in arid Australia with long rainfall records and *C. glaucophylla* populations nearby, showing periods where this exceeds 20 mm. For clarity, the y-axis is truncated below 20 mm. The value of 30 mm, likely to provide good climatic conditions for *C. glaucophylla* seedling establishment, is indicated by the dotted line.



Appendix 1(a) Comparison of 24-mo moving average rainfall for five stations in the region, arranged from the northern-most (top panel) to the southern-most station (bottom panel). Possible threshold values for *C. glaucophylla* regeneration of 20 and 30 mm rain per month are shown by the dotted lines. Mean annual rainfall is shown for each station, although note that the measurement periods differ.



Appendix 1(b) 24-mo moving average rainfall between 1990 and 2016 for rainfall stations closest to Arid Recovery Reserve. Olympic Dam, the nearest station, has only a short rainfall record, during which the station was moved. Data are similar to those from Andamooka (approx. 30 km east) and Roxby Downs Station (Roxby HS) (approx. 26 km south-west). Possible threshold values for *C. glaucophylla* regenaration of 20 and 30 mm rain per month are shown by the dotted lines.



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834

835 **Appendix 2.** (a) The relationship between height and basal diameter for *C. glaucophylla* trees
836 in the Roxby Downs region. The red triangles represent 'young' trees (seedlings, saplings and
837 those with a slim, erect form), the filled circles are those noted as being single stem with a
838 good form (straight, approximately circular stem), and the open circles are the remaining
839 trees, most multi-stemmed and many gnarled and twisted. The line was fitted to only the solid
840 symbols (young and single-stemmed trees). (b) The relationship between diameter at breast
841 height and basal diameter for *C. glaucophylla* trees in the Roxby Downs region.

Appendix 3. Radiocarbon Results

Lab ID	Sample ID	Distance from bark (mm)	$\delta^{13}C$ (‰)	pMC		^{14}C Age (BP)		Unmodelled Cal ages (AD)							Modelled Cal ages (AD)						A_{model}
				Mean	1σ	Mean	1σ	1σ range		2σ range		Mean	1σ	Median	1σ range		2σ range		Mean	1σ	Median	
-	RD1 3B - Bark	0																	2009	0		
OZU137	RD1 3B - Sample 1	37	-19.6	96.85	0.33	255	30	1646	1953	1636	1954	1722	69	1743	1951	1954	1746	1955	1941	42	1952	
OZU138	RD1 3B - Sample 2	83	-19.1	98.28	0.27	140	25	1699	1945	1692	1949	1841	79	1857	1863	1949	1711	1951	1886	55	1896	61%
OZU139	RD1 3B - Sample 3	127	-19.2	97.89	0.25	170	20	1678	1951	1672	1955	1809	89	1818	1798	1879	1676	1940	1832	51	1840	
OZU140	RD1 3B - Sample 4	171	-18.6	96.55	0.37	280	30	1530	1953	1510	1954	1662	81	1652	1767	1799	1658	1801	1772	35	1786	
OZU141	RD1 3B - Sample 5	217	-19.4	97.22	0.28	225	25	1666	1798	1652	1954	1751	60	1758	1742	1789	1651	1796	1749	40	1760	
-	RD2 9B - Bark	0																	2009	0		
OZU142	RD2 9B - Sample 1	39	-18.5	149.55	0.46	Modern		1971	1972	1970	1972	1971	1	1971	1971	1972	1964	1972	1971	2	1971	
OZU143	RD2 9B - Sample 2	75	-20.3	97.80	0.34	180	30	1674	1954	1669	1955	1801	87	1802	1934	1955	1867	1955	1933	27	1942	94%
OZU144	RD2 9B - Sample 3	115	-19.3	97.98	0.32	165	30	1682	1949	1674	1955	1819	87	1838	1871	1951	1838	1952	1909	39	1924	
OZU145	RD2 9B - Sample 4	152	-18.6	98.25	0.29	140	25	1698	1946	1689	1950	1839	80	1855	1850	1945	1806	1948	1883	50	1890	
OZU146	RD2 9B - Sample 5	192	-18.0	97.96	0.35	165	30	1680	1949	1673	1955	1817	87	1835	1803	1937	1678	1946	1854	63	1864	
-	RD3 2A - Bark	0																	2009	0		
OZU147	RD3 2A - Sample 1	33	-19.9	111.31	0.38	Modern		1996	1998	1958	1998	1993	11	1997	1996	1998	1995	1998	1997	1	1997	
OZU148	RD3 2A - Sample 2	79	-21.2	138.52	0.45	Modern		1975	1975	1963	1976	1973	5	1975	1974	1976	1963	1976	1973	4	1975	66%
OZU149	RD3 2A - Sample 3	124	-19.4	96.87	0.28	255	25	1648	1796	1642	1954	1723	67	1744	1952	1954	1781	1955	1940	46	1952	
OZU150	RD3 2A - Sample 4	170	-20.2	97.77	0.25	180	25	1674	1954	1670	1955	1792	88	1781	1938	1953	1694	1954	1924	58	1946	
OZU151	RD3 2A - Sample 5	220	-20.2	97.97	0.24	165	20	1683	1949	1676	1955	1818	88	1841	1925	1950	1680	1952	1907	67	1934	

Note: Simple sequence deposition model of the OxCal program (Bronk Ramsey 2008) was used for age-depth modelling. Radiocarbon calibration data used in the model were the SH Zone 1-2 Bomb data (Hua *et al.* 2013) extended back in time using the SHCal13 data (Hogg *et al.* 2013). All three models were good, as the overall model agreement indexes ranged from 61 to 94%, which are higher than the accepted level of 60% (Bronk Ramsey 2008)

References for Appendix 3.

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